

Estimation of heritability from varietal trials data

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Abstract. We present the estimation of heritabilities of an observed trait in situations where evaluation of several pure breeding lines is performed in a trial at a single location and in trials from several locations. For the single location situation, we evaluate exact confidence intervals, the probability of invalid estimates, and the percentage points of the distribution of heritability. Simulations were performed to numerically verify the results. Additionally, approximations to the bias and standard error of the estimate were obtained and are presented along with their simulated values and coefficients of skewness and kurtosis. For trials in several locations, explicit expressions for exact values of confidence limits are not available. Further, one would require knowledge of one more parameter, represented by the ratio of genotype \times environment (G \times E) interaction variance to error variance, in addition to the number of genotypes, replication and true heritability value. Approximations were made for bias and the standard error of estimates of heritability. The evaluation of the distribution of heritability and its moments was recognized as a problem of the linear function of an independent chi-square. The methods have been illustrated by data from experiments on grain and straw yield of 64 barley genotypes evaluated at three locations.

Key words: Heritability – Standard error – Genotype × environment interaction – Confidence interval – Invalid estimates

Introduction

An assessment of the heritability of various traits is of considerable importance in crop improvement programs; for example, to predict response to selection. Estimates of heritability are available in several experimental situations, but the standard errors of these estimates, or the confidence intervals of heritability, have been reported mostly for parent-offspring data (Gravbill et al. 1956: Bogyo and Becker 1963; Broemeling 1969). Falconer (1982, pp 165-167) gave a large sample standard error where the heritability was obtained from the regression of offspring on parents. Exact confidence intervals for heritability were obtained by Knapp et al. (1985) when the data were collected on a progeny-mean basis from several environments. The standard errors and confidence intervals of response to selection were given by Bridges et al. (1991). General formulae for the ratio of variances were provided by Graybill et al. (1956) for parent-offspring data and Graybill and Wang (1979) for a two-factor nested model.

The purpose of the present paper is to provide expressions for the standard errors of the estimate of heritability from the analysis of variance on data generated in a randomized complete block design conducted in one environment (or single trial) and in several environments (or multi-locational trials). This paper also studies the behavior of the distribution of heritability, using simulation techniques. Barley data have been used to illustrate the methodology.

Materials and methods

Estimation of heritability in a single trial

Consider estimating the heritability h^2 of a trait Y from the responses of a set of v inbred lines, chosen randomly to represent a population of lines, when grown in b randomized complete blocks in a single trial. Let y_{ij} be the response of the i-th genotype grown in the j-th block (i=1, 2, ..., v, j=1, 2, ..., b). A model for y_{ij} and the parameters involved is

$$\mathbf{y}_{ij} = \boldsymbol{\mu} + \mathbf{g}_i + \boldsymbol{\beta}_j + \boldsymbol{\varepsilon}_{ij} \tag{1}$$

where μ is general mean, g_i represents the effect of i-th genotype and is assumed to be independent and normally distributed with zero mean and variance σ_g^2 , β_j is the unknown fixed effects of the j-th block, and ε_{ij} values are experimental errors assumed to be independently normally distributed with zero mean and variance σ_e^2 (i = 1, ..., v; j = 1, 2, ... b). Broad sense heritability (h^2) of a trait is the ratio of genetic variability (σ_g^2) to phenotypic variability ($\sigma_e^2 + \sigma_e^2$) and is given by

$$h^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_g^2) . \tag{2}$$

Generally, estimation of variance components is based on analysis-of-variance (ANOVA) estimates obtained as outlined in Table 1. Estimates of σ_e^2 and σ_e^2 are

$$\hat{\sigma}_{e}^{2} = M_{e}$$
 and $\hat{\sigma}_{g}^{2} = (M_{g} - M_{e})/b$.

An estimate

Thus an estimate \hat{h}^2 of heritability h^2 is

$$\hat{h}^2 = \hat{\sigma}_g^2 / (\hat{\sigma}_e^2 + \hat{\sigma}_g^2) = (V_r - 1) / (V_r + b - 1)$$
(3)

where $V_{\rm r}\!=\!M_{\rm g}\!/M_{\rm e}$ is the variance ratio. Note that the exact distribution of

W = V_r
$$\sigma_e^2 / (\sigma_e^2 + b \sigma_g^2) = V_r / [1 + b h^2 (1 - h^2)^{-1}]$$

is the F distribution with q=v-1 and f=(v-1)(b-1) df. Thus the exact distribution of \hat{h}^2 can easily be traced. We know that the estimate \hat{h}^2 is biased for h^2 and may assume negative (invalid) values. The amount of bias is of interest to plant breeders. We give expressions for bias, standard error, probability of invalid estimates, and confidence interval below. Appendix I gives the method of obtaining them and the expressions for the coefficients involved but not reproduced in this section.

Bias
$$b(\hat{h}^2) = 2(1-h^2)[1+(b-1)h^2][1+(b-2)h^2]/(h^2 bf)$$
.
Standard error $SE(\hat{h}^2) = (1-h^2)[1+(b-1)h^2][2/(bf)]^{1/2}$.
Probability of invalid estimate $H[q, f, (1+b\lambda^2)^{-1}]$.
Probability distribution of \hat{h}^2 $H[q, f, y]$.
 $100(1-\alpha)\%$ confidence interval $(\hat{h}_L^2, \hat{h}_U^2)$ where
 $\hat{h}_L^2 = (V_r - F_U)/[V_r + (b-1)F_U]$
 $\hat{h}_U^2 = (V_r - F_L)/[V_r + (b-1)F_L]$.

An estimate of bias in \hat{h}^2 can be obtained by substituting the estimate of h^2 . This estimate can be subtracted from \hat{h}^2 to correct for the bias. Several statistical packages and libraries of mathematical subroutines contain the evaluation of the probability of lower tail or percentage points of the F distribution and may facilitate the computations in this section. In order to evaluate the upper α probability point of the distribution of \hat{h}^2 , let y_α be the upper α probability point of the F distribution with q and f df, i.e., $\operatorname{Prob}(F_{q,f} > y_\alpha) = \alpha$, then the corresponding point \hat{h}^2_α for heritability \hat{h}^2 is $h^2_\alpha = [(1 + b \lambda^2) y_\alpha - 1]/[(1 + b \lambda^2) y_\alpha + b - 1]$. Further, in order to test a given value of heritability, say h^2_0 , one may compute the exact probability level = $\operatorname{Prob}(\hat{h}^2 > h^2_0) = 1 - H(q, f, u)$, where $u = [1 + b h^2_0/(1 - h^2_0)]/[1 + b h^2/(1 - h^2)]$.

The standard error (SE) gives a measure of the precision of the estimate. In cases where confidence intervals are reported, the SE of \hat{h}^2 may not be necessary. For situations, where the distribution of \hat{h}^2 approximates to the normal distribution, then evaluation of SE (\hat{h}^2) is required to obtain the sampling distribution of the estimate. If several independent estimates of heritability are to be combined, the standard errors determine the weights used in the pooled estimate of heritability. Further, SE (\hat{h}^2) does not require any additional parameter, such as a confidence coefficient in the confidence interval.

Table 1. Analysis of variance for single location data

| Source | df | Mean square | Expected mean square Not relevant $\sigma_e^2 + b \sigma_g^2 \sigma_e^2$ | |
|-----------------------------|------------------------------|--|---|--|
| Block Genotypes Error | b-1 q=v-1 f=(v-1)(b-1) | Not relevant M _g M _e | | |

Table 2. Analysis of variance for multilocation data

| Source | df | Mean square | Expected mean square |
|----------------------|------------------------|----------------|--|
| Environ- ment (E) | L-1 | Not relevant | |
| Blocks/ env. | (r-1) L | Not relevant | |
| Genotype (G) | q = v - 1 | M _g | $\sigma_{\rm e}^2$ + b $\sigma_{\rm I}^2$ + b L $\sigma_{\rm g}^2$ |
| G×E | (v-1)(L-1) | Mι | $\sigma_{\rm e}^2 + b \sigma_{\rm I}^2$ |
| Error | f = (v-1) · (b-1) L | M_{e} | σ_{e}^{2} |

Estimation of heritability from multi-location trials

Consider a series of trials conducted in randomised complete block design with v genotypes and b replications, over L environments. Let h^2 be the heritability of trait Y on which we observed y_{ijk} as the response from i-th genotype (i = 1, ..., v), j-th block (j = 1, ..., b) over the k-th environment (k = 1, ..., L). The model for y_{ijk} is

$$y_{ijk} = \mu + g_i + \alpha_k + \delta_{ik} + \beta_{ik} + \varepsilon_{ijk}$$
(4)

where μ is the general mean, g_i is the effect of i-th genotype, α_k is the effect of the k-th environment, δ_{ik} is the interaction effect between the i-th genotype and the k-th environment, and β_{jk} is the effect of the j-th block within the k-th environment. The effects g_i s, δ_{ik} s, and ε s are assumed to be independently and randomly distributed with zero means and variances σ_g^2 , σ_I^2 and σ_e^2 . The heritability of trait Y, denoted by h^2 , is defined as

$$h^{2} = \sigma_{g}^{2} / (\sigma_{g}^{2} + \sigma_{I}^{2} + \sigma_{e}^{2}) .$$
 (5)

Estimation

To estimate h^2 we construct an ANOVA table (Table 2).

Expected values of mean the square appear similar to those given in Table 2, for any of the following three models: (1) genotypic effects fixed and environment random where σ_g^2 = variance of the fixed genotypes, (2) genotype random and environment fixed, and (3) both genotype and environment random. The variance components are estimated as

$$\hat{\sigma}_{e}^{2} = M_{e}, \sigma_{I}^{2} = (M_{I} - M_{e})/b \text{ and } \sigma_{e}^{2} = (M_{e} - M_{I})/(b L).$$

Let us define the two variance ratios as

$$V_g = M_g/M_I$$
 and $V_I = M_I/M_e$

Thus an estimate of h² is

$$\begin{split} \hat{h}^2 &= \hat{\sigma}_g^2 / (\hat{\sigma}_g^2 + \hat{\sigma}_I^2 + \hat{\sigma}_e^2) \\ &= (M_g - M_I) / [M_g + (L-1) M_I + L(b-1) M_e] \\ &= (V_g - 1) / [V_g + L - 1 + L(b-1) / V_I]. \end{split}$$

(6)

| Item | | Grain yield Trials | Grain yield Trials | | Straw yield Trials | Straw yield Trials | | |
|--|------------------------|------------------------------|------------------------------|---------------------------|-----------------------------|-------------------------------|-----------------------------|--|
| | | 1 | 2 | 3 | 1 | 2 | 3 | |
| Mean squar | res | | | | | | | |
| Source | df | Mean squa | res | | | | | |
| Blocks Genotype Error $(\hat{\sigma}_{e}^{2})$ | 2 63 126 | 633,095 509,155 58,801 | 143,392 249,945 19,268 | 61,707 51,668 7,010 | 51,691 263,573 82,794 | 1,130,316 94,976 45,866 | 194,008 89,148 32,124 | |
| Variance co | mponent esti | mates | | | | | | |
| $\hat{\sigma}_{g}^{2}$ | | 58,801 150,118 | 19,268 76,892 | 7,010 14,886 | 82,794 60,260 | 45,866 16,370 | 32,124 19,008 | |
| Estimates o | f heritability | | | | | | | |
| \hat{h}^2 | | 0.72 | 0.80 | 0.68 | 0.42 | 0.26 | 0.37 | |
| 95% confid | ence interval | S | | | | | | |
| Lower Upper | | 0.6112 0.8068 | 0.7160 0.8653 | 0.5630 0.7781 | 0.2685 0.5698 | $0.1090 \\ 0.4270$ | 0.2171 0.5265 | |
| 99% confid | ence interval | s | | | | | | |
| Lower Upper | | 0.5726 0.8298 | 0.6850 0.8820 | 0.5219 0.8040 | 0.2201 0.6127 | 0.0628 0.4771 | 0.1689 0.5720 | |
| SE, bias, sk | ewness and k | turtosis | | | | | | |
| Approx. sê Simul. sê (ĥ | $(\hat{\mathbf{h}}^2)$ | 0.0499 0.0524 | 0.0379 0.0402 | 0.0550 0.0575 | 0.0776 0.0796 | 0.0818 0.0832 | $0.0797 \\ 0.0861$ | |
| Approx. bia Simul. bias | S | 0.0087 - 0.0052 | 0.0062 - 0.0045 | 0.0099 - 0.0054 | 0.0191 - 0.0045 | 0.0286 - 0.0027 | 0.0214 - 0.0041 | |
| Simul. skew Simul. kurte | ness osis | -0.72 0.27 | -0.83 0.43 | -0.67 0.20 | -0.35 -0.12 | -0.14 -0.23 | -0.29 -0.15 | |

Table 3. Analysis of variance on grain and straw yields from three trials together with estimates of heritabilities

Approx.: approximated values. Simul.: simulated values based on 2,000 runs

The distribution of \hat{h}^2 is based on three independent quadratic forms (M_g, M₁, M_e) or on two dependent variance ratios V_g and V_I (see Appendix II). If h^2 is based on progeny means (Knapp et al. 1985), then the heritability estimate is expressed only in terms of V_g; therefore its distribution is determined as in the previous section. The probability distribution of \hat{h}^2 can be expressed as that of a linear combination of independent chi-square variables. Its distribution, however, depends on four parameters (v, b, L and λ_1^2) in addition to h^2 where $\lambda_1^2 = \sigma_1^2 / \sigma_e^2$ the ratio of G × E interaction variance to error variance. A brief derivation of the results presented in the following is in Appendix II.

Bias $h^2 [C_{11}/A_1 - C_{12}/(A_1 A_2)]$

Standard error
$$h^2 [C_{11}/A_1^2 + C_{22}/A_2^2 - 2 C_{12}/(A_1 A_2)]^{1/2}$$

Probability of invalid estimate H[q, p, $(1 + b \lambda_1^2)/(1 + b \lambda_1^2 + b L \lambda_g^2)$].

Probability distribution $\operatorname{Prob}(\chi_{\nu}^2 > Z)$

 $\begin{array}{l} 100(1-\alpha)\,\%\,asymptotic\,\,confidence\,\,interval\\ [\hat{h}^2-Z_{\alpha/2}\,\,SE\,(\hat{h}^2),\,\hat{h}^2+Z_{\alpha/2}\,\,SE\,(\hat{h}^2)] \end{array}$

Heritability in terms of
$$\lambda_g^2$$
 and λ_I^2
h² = $\lambda_g^2/(\lambda_g^2 + \lambda_I^2 + 1)$, where $\lambda_g^2 = \sigma_g^2/\sigma_e^2$

Obtaining exact confidence limits for h^2 appears to be cumbersome, since it involves two ratios $(\lambda_1^2 \text{ and } \lambda_g^2)$ whose estimates are not independent, if we take the ratios of mean squares. An asymptotic confidence interval is given in the above using an asymptotic standard error and percentage points $Z_{\alpha/2}$ of the standard normal distribution.

Results and discussion

Sixty four genotypes from three trials were evaluated in randomized complete block designs with three replications at three locations (Tel Hadya, Bouider and Breda) in Syria. These trials were conducted by the Cereals Program, ICARDA. Data on straw and grain yields were collected during May, 1990. The analyses of these data SE

Bias

| Mean squares | | | | | |
|--------------------------------|-------------|------------------------|------------------------|--|--|
| Source | df | Grain yield | Straw yield | | |
| Location (L) | 2 | 1.314×10^{8} | 1.153×10^{8} | | |
| Blocks/Loc | 6 | 2.794×10^{5} | 4.587×10^{5} | | |
| Genotype (G) | 63 | 5.127×10^{5} | 2.078×10^{5} | | |
| G×L | 126 | 1.490×10^{5} | 1.200×10^{5} | | |
| Error $(\hat{\sigma}_{e}^{2})$ | 378 | 2.836×10^4 | 5.359×10^4 | | |
| Variance com | ponent es | stimates | | | |
| $\hat{\sigma}^2$ | | 4.0411×10^{4} | 0.9756×10^{4} | | |
| $\hat{\sigma}_{r}^{2}$ | | 4.0213×10^{4} | 2.2137×10^{4} | | |
| $\hat{\sigma}_{e}^{2}$ | | 2.8360×10^4 | 5.3590×10^4 | | |
| Estimates of I | heritabilit | y and standard error | 's | | |
| $\hat{\mathbf{h}}^2$ | | 0.3710 | 0.1140 | | |

Table 4. Combined analysis of variance of the three trials and estimation of heritability

for an estimation of heritability are given in Tables 3 and 4.

0.0680

0.0160

0.1140

0.0490

0.0220

The standard errors approximated from the formula in (4) are reasonable close to the corresponding simulated values. Relativey low magnitudes of skewness and kurtosis values indicate that the distribution of estimates of heritability can be reasonably approximated by the normal distribution. However, the approximated and simulated biases are similar and low magnitude for high values of heritabilities.

Appendix I

Bias and standard error of \hat{h}^2

An approximation to the bias is obtained using Taylor's series expansion (Kendall and Stuart 1969).

Bias $(\hat{h}^2) = E(\hat{h}^2) - h^2 = E(N/D) - h^2$

where the numerator $N = M_g - M_e$ and the denominator $D = M_{g} + (b-1) M_{e}$. An approximation of the bias is

$$B(\hat{h}^{2}) = [E(N)/E(D)] \cdot \{var(N)/[E(N)]^{2} - cov(N, D)/[E(N) \cdot E(D)]\}.$$

The expected value of random variable χ^2_ν is ν with a variance 2v; further, $q M_g \sim (\sigma_e^2 + b \sigma_g^2) \chi_q^2$ and $f M_e \sim \sigma_e^2 \chi_f^2$, where q = v - 1, f = q(b-1). We obtain the expectations, variances and covariances of N and D as

$$E(N) = b \sigma_g^2 = b \lambda \sigma_e^2$$
, where

$$\lambda = \sigma_g^2 / \sigma_e^2 = h^2 / (1 - h^2)$$
 expressed in terms of h²,

$$E(D) = b (\sigma_e^2 + \sigma_g^2) = b \sigma_e^2 / (1 - h^2),$$

$$var(N) = var(M_g) + var(M_e) = 2(\sigma_e^2 + b \sigma_g^2)^2 / q + 2\sigma_e^4 / f$$

= 2\sigma_e^4 [(1 + b \lambda^2)^2 / q + 1/f],

var (D) =
$$2\sigma_{\rm e}^4 [(1+b\lambda^2)^2/q + (b-1)^2/f]$$
,

 $\operatorname{cov}(\mathbf{N}, \mathbf{D}) = 2\sigma_e^4 \left[(1 + b \ L^2)^2 / q - (b - 1) / f \right].$

After algebraic simplification, we get

$$B(\hat{h}^2) = 2(1-h^2) [1+(b-1)h^2] [1+(b-2)h^2]/(h^2 b f).$$

The mean square error (or variance ignoring bias) of \hat{h}^2 is given by

$$var(\hat{h}^{2}) = [E(N)/E(D)]^{2} \{var(N)/[E(N)^{2} + var(D)/[E(D)]^{2} - 2 \operatorname{cov}(N, D)/[E(N) E(D)]\}$$
$$= 2(1-h^{2})^{2} [1+(b-1) h^{2}]^{2}/(b f).$$

Probability of a negative estimate of h^2

Since \hat{h}^2 has a difference expression, $M_g - M_e$, as its numerator, which may sometimes be negative, this results in an invalid estimate of h². The probability of such cases (Gill and Jensen 1968) is given by

$$Prob(h^{2} < 0) = Prob(M_{g} < M_{e}) = Prob(V_{r} < 1)$$
$$= Prob[W < \sigma_{e}^{2}/(\sigma_{e}^{2} + b \sigma_{g}^{2})]$$
$$= Prob[W < (1 + b \lambda^{2})^{-1}]$$
$$= H[q, f, (1 + b \lambda^{2})^{-1}]$$

where $H[n_1, n_2, x]$ is the lower-tail probability at point x of the F distribution with n_1 and n_2 df and $\lambda^2 = h^2/2$ $(1-h^2)$. The integral form of H[n₁, n₂, x] is

$$H[n_1, n_2, x] = \int_0^x [B(n_1/2, n_2/2)]^{-1} (n_1/n_2)^{n_1 1/2} \cdot y^{(n_1/2) - 1} (1 + n_1 y/n_2)^{-(n_1 + n_2)/2} dy$$

and B(n,m) is the beta function.

Probability distribution of \hat{h}^2

The exact probability distribution of \hat{h}^2 is

$$\begin{aligned} \operatorname{Prob}(\hat{h}^2 < x) &= \operatorname{Prob}[(V_r - 1)/(V_r + b - 1) < x] \\ &= \operatorname{Prob}(w < y) = H[q, f, y] \\ \end{aligned}$$
 where $y = [1 + x \ b/(1 - x)]/(1 + b \ \lambda^2).$

Confidence interval

To compute the $100(1-\alpha)\%$ confidence interval for h^2 , let F_L and F_U be respectively the $\alpha/2$ and $1-\alpha/2$ lower probability points of the F distribution with (q, f) degrees of freedom. Using the distributional behavior of W as the F distribution, it is easy to translate

$$\operatorname{Prob}(\mathbf{F}_{L} \leq W \leq \mathbf{F}_{U}) = 1 - \alpha$$

into

Prob
$$[(V_r - F_U)/(V_r + (b-1) F_U) \le h^2$$

 $\le (V_r - F_I)/(V_r + (b-1) F_I)] = 1 - \alpha$.

Thus an exact $100(1-\alpha)$ % confidence interval is $(\hat{h}_L^2, \hat{h}_U^2)$, where

$$\hat{h}_{L}^{2} = (V_{r} - F_{U})/[V_{r} + (b-1) F_{U}]$$

and

$$h_{\rm U}^2 = (V_{\rm r} - F_{\rm L}) / [V_{\rm r} + (b - 1) F_{\rm L}].$$

Appendix II

Evaluation of bias, standard error, and the probability of a negative estimate of heritability from multi-location trials.

Dependence of V_a and V_I

Compute the covariance $cov(V_g, V_I)$

$$cov(V_{g}, V_{l}) = E(V_{g}, V_{l}) - E(V_{g}) E(V_{e})$$
$$= E\left(\frac{M_{g}}{M_{l}} \cdot \frac{M_{l}}{M_{e}}\right) - E\left(\frac{M_{g}}{M_{l}}\right) E\left(\frac{M_{I}}{M_{e}}\right)$$
$$= E(M_{g}) E\left(\frac{1}{M_{e}}\right) - E(M_{g}) E\left(\frac{1}{M_{l}}\right) E(M_{l}) E\left(\frac{1}{M_{e}}\right)$$
$$= E(M_{g}) E\left(\frac{1}{M_{g}}\right) \left[1 - E(M_{l}) E\left(\frac{1}{M_{l}}\right)\right] \neq 0.$$

Bias and mean square error of \hat{h}^2

We shall follow the Taylor series expansion approach on \hat{h}^2 in terms of the numerator $N = M_g - M_I$ and denominator $D = M_g + (L-1) M_I + L(b-1) M_e$. Notice that $E(N) = b L \lambda_g^2 \sigma_e^2$, and $E(D) = b L \sigma_e^2(\lambda_g^2 + \lambda_I^2 + 1)$.

$$\mathbf{B}(\hat{\mathbf{h}}^2) = \mathbf{E}(\hat{\mathbf{h}}^2) - \mathbf{h}^2 = \mathbf{h}^2 \left[\mathbf{C}_{11} / \mathbf{A}_1 - \mathbf{C}_{12} / (\mathbf{A}_1 \mathbf{A}_2) \right],$$

$$\operatorname{var}(\hat{h}^2) = h^4 \left[C_{11} / A_1^2 + C_{22} / A_2^2 - 2C_{12} / (A_1 A_2) \right]$$

where $A_1 = b L \lambda_g^2$, $\lambda_g^2 = \sigma_g^2 / \sigma_e^2$, and the ratio of genetic variance to error variance components, $A_2 = b L (\lambda_g^2 + \lambda_1^2 + 1)$,

$$\begin{split} \mathrm{C}_{11} &= 2 \left[(1 + b \,\lambda_{\mathrm{I}}^2 + b \,\mathrm{L}\,\lambda_{\mathrm{g}}^2)^2 / \mathrm{q} + (1 + b \,\lambda_{\mathrm{I}}^2)^2 / \mathrm{b} \right], \\ \mathrm{C}_{22} &= 2 \left[(1 + b \,\lambda_{\mathrm{I}}^2 + b \,\mathrm{L}\,\lambda_{\mathrm{g}}^2)^2 / \mathrm{q} + (\mathrm{L} - 1)^2 \,(1 + b \,\lambda_{\mathrm{I}}^2)^2 / \mathrm{b} \right. \\ &\quad + \mathrm{L}^2 \,(\mathrm{b} - 1)^2 / \mathrm{f} \right], \\ \mathrm{C}_{12} &= 2 \left[(1 + b \,\lambda_{\mathrm{I}}^2 + b \,\mathrm{L}\,\lambda_{\mathrm{g}}^2)^2 / \mathrm{q} - 2 (\mathrm{L} - 1) \,(1 + b \,\lambda_{\mathrm{I}}^2)^2 / \mathrm{b} \right]. \end{split}$$

The heritability in terms of λ_g^2 and λ_I^2 is

$$h^2 = \lambda_g^2 / (\lambda_g^2 + \lambda_I^2 + 1).$$

Probability of negative estimates of h^2

The quantity h^2 would be estimated as negative if $M_g < M_I$. Thus,

$$\begin{aligned} \operatorname{Prob}(\hat{h}^2 < 0) &= \operatorname{Prob}(M_g < M_I) \\ &= \operatorname{Prob}[W < (\sigma_e^2 + b \sigma_I^2) / (\sigma_e^2 + b \sigma_I^2 + b L \sigma_g^2)] \end{aligned}$$

where $W = [M_g/(\sigma_e^2 + b \sigma_I^2 + b L \sigma_g^2)]/[M_I/(\sigma_e^2 + b \sigma_I^2)]$ and would follow the F-distribution with q and p df. Thus

Prob (h² < 0) = H [q, p, (1 + b $\lambda_{I}^{2})/(1 + b \lambda_{I}^{2} + b L \lambda_{g}^{2})]$.

Probability distribution of \hat{h}^2

We can express the probability $Prob(\hat{h}^2 > x)$ as a probability on a linear combination of independent chi-squares variables.

Prob (
$$\hat{h}^2 > x$$
)
= Prob {($M_g - M_I$)/[$M_g + (L-1) M_I + L(b-1) M_e$] > x}.
Since $\alpha M_{\infty} (1 + b \lambda^2 + b I_{\infty} \lambda^2) \sigma^2 x^2$ $p M_{\infty} (1 + b \lambda^2 + b I_{\infty} \lambda^2)$

Since $q M_g \sim (1 + b \lambda_I^2 + b L \lambda_g^2) \sigma_e^2 \chi_q^2$, $p M_I \sim (1 + b \lambda_I^2 + b L \lambda_g^2) \sigma_e^2 \chi_q^2$, $p M_I \sim (1 + b \lambda_I^2) b^{-1} \sigma_e^2 \chi_p^2$, and $f M_e \sim \sigma_e^2 \chi_I^2$. We have, after simplification,

 $Prob(\hat{h}^2 > x) = Prob(\theta_1 \chi_q^2 + \theta_2 \chi_p^2 + \theta_3 \chi_f^2 > 0).$

Following an approximation given by Imhoff (1961), the above probability can be approximated by Prob ($\chi_{\nu}^2 > Z$), as a probability function having a chi-square distribution where

$$\begin{split} \nu &= C_2^3/C_3^3 \,, \\ z &= -C_1 \, (\nu/C_2)^{1/2} + \nu \,, \\ C_1 &= \theta_1 \, q + \theta_2 \, p + \theta_3 \, f \,, \\ C_2 &= q \, \theta_1^2 + p \, \theta_2^2 + f \, \theta_3^2 \,, \\ C_3 &= q \, \theta_1^3 + p \, \theta_2^3 + f \, \theta_3^3 \,. \end{split}$$

Thus the probability point of the \hat{h}^2 distribution can be obtained by using a suitable numerical algorithm.

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